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A REVISION OF THE PUNCTATUS GROUP OF AFRICAN $TYPHLOPS \ (REPTILIA: SERPENTES)$

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No. 6—A Revision of the PUNCTATUS Group of African TYPH-LOPS (Reptilia: Serpentes)

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CONTENTS

	rage
Introduction	389
New taxonomic arrangement	391
Characters examined	392
Recognition of "non-dimensional" species	399
Allopatric relationships	403
Systematic account	411
Typhlops punctatus punctatus (Leach)	411
Typhlops punctatus liberiensis (Hallowell)	412
Typhlops congestus (Duméril and Bibron)	413
Typhlops boulengeri boulengeri Bocage	414
Typhlops boulengeri usambaricus subsp.n.	416
Typhlops gierrai Mocquard	417
Typhlops schmidti schmidti Laurent	417
Typhlops schmidti tanganicanus subsp.n.	418
Tuphlops rondoensis Loveridge	
	419
Typhlops obtusus Peters	420
Typhlops fornasinii Bianconi	421
Typhlops steinhausi Werner	422
Typhlops angolensis Bocage	422
Phylogenetic relationships	426
Key to the species	432
References	434

INTRODUCTION

For a very long time no herpetologist appears to have been aware that the "nearly panethiopian species," Typhlops punctatus, concealed a problem. Only K. P. Schmidt (1923) understood that different forms were being confused under this name; thus he was able to discriminate three different species in Lang and Chapin's beautiful collection. Subsequent authorities, however, especially Loveridge and Bogert, not only did not follow him but insisted that these forms were only individual or color variants.

However, when I had to study my own snake material (Laurent, 1956), collected in the western Graben (eastern Congo and Ruanda-Urundi), I came to the conclusion that K. P. Schmidt had been perfectly right, and that his only error had been that he distinguished only three species when he had four species in hand. There were indeed nomenclatorial discrepancies, as appears in the comparison below:

Schmidt 1923	Laurent 1956
$Typhlops\ congestus$	(Typhlops congestus
	(Typhlops punctatus
$Typhlops\ intermedius$	Typhlops angolensis angolensis
Typhlops punctatus	Typhlops boulengeri

In my 1956 paper, I showed that these species have little geographic variation in the territory of the former Belgian Congo, with the remarkable exception of T. angolensis whose savanna and mountain populations are conspicuously differentiated.

The following subspecies of *angolensis* were recognized: *adolfi* Sternfeld in lowland savannas, *dubius* Chabanaud in highland savannas, *symoensi* Laurent in savanna highlands of Itombwe (southern Kivu), *polylepis* Laurent in mountain and transition forest on the western side of the western mountains of the Graben, *irsaci* Laurent in mountain forests of the eastern side of the same highlands and in the Rugege forest (Ruanda).

In 1956, however, I wrongly eonsidered as valid some forms such as congicus Peters and lestradei Witte, which I have since synonymized, respectively, with angolensis Bocage and dubius Chabanaud. Those nominal forms were based on specimens whose eyes were hidden under head scales. Loveridge (1942) realized that this character was not necessarily significant and for that reason considered lestradei as a subspecies of blanfordi. In many species in which the eye is normally distinguishable some specimens may have a lacteous opaque hue and hidden eyes; the proportions of head scales are also different and this correlation has been mistaken for a taxonomic character. In 1960, I suggested that this condition occurred immediately preceding sloughing and can occur in any species.

A revision of the whole Typhlops collection in the Musée Royal de l'Afrique Centrale (Tervuren) might have permitted further study of geographical variation in west Africa and increased our knowledge of the distributions towards the west and the south, but I have not had the opportunity to undertake it. On the other

 390°

hand, the collections of the Museum of Comparative Zoology have offered the possibility of examining the situation in other regions of Africa and this, in fact, is more interesting. This investigation, supplemented by the examination of the pertinent material in the Chicago Natural History Museum (CNHM), the American Museum of Natural History (AMNH), and the United States National Museum (USNM), is the subject of the present paper.

The material studied comprises numerous specimens labeled as *Typhlops punctatus*, *T. p. gierrai*, *T. blanfordi blanfordi*, *T. blanfordi*, *T. blanfordi*, *T. blanfordi*, *T. tettensis*, *T. tettensis*,

NEW TAXONOMIC ARRANGEMENT

1. *Typhlops punctatus punctatus* (Leach)—Savanna populations in the Sudanese subprovince.

2. Typhlops punctatus liberiensis (Hallowell)—Forest populations in the Liberia-Ghana region.

3. *Typhlops congestus* (Duméril and Bibron)—Forest populations of the Cameroon and Congo area.

Typhlops congestus and T. punctatus may perhaps be one polytypic species whose terminal races behave, between themselves, like good species. There is, however, at present, no evidence of intergradation between congestus and liberiensis.

4. Typhlops boulengeri boulengeri Bocage—Savanna species with a circum-forest distribution, sympatric with T. punctatus in the Sudanese subprovince. The East African material referred to punctatus is actually boulengeri.

5. Typhlops boulengeri usambaricus subsp. n.—A spotted and mountain subspecies of T. boulengeri.

6. *Typhlops gierrai* Mocquard—A mountain species sympatric with *usambaricus* which it resembles by its frequently spotted pattern.

7. Typhlops schmidti schmidti Laurent—A savanna species from southern Congo, eastern Angola and northern Rhodesia.

8. Typhlops schmidti tanganicanus subsp. n.—A recognizable subspecies from southern Tanganyika and northern Mozambique =T. tettensis tettensis Loveridge (non Peters).

9. Typhlops rondoensis Loveridge—This form described as a subspecies of tettensis seems to be a species distinct from schmidti and it is entirely different from the true tettensis which is a synonym of fornasinii.

10. Typhlops fornasinii Bianconi—A very distinct species possibly related to *T. angolensis (tettensis* Peters and mossambicus Peters appear to be synonyms).

11. Typhlops obtusus Peters—A species quite distinct from tettensis, and related to T. angolensis. Investigation of material from northern Rhodesia and Katanga may yet prove that the whole angolensis complex may be conspecific with obtusus.

12. Typhlops steinhausi Werner—A forest form from Cameroon and Congo.

13. Typhlops angolensis angolensis Bocage—A forest form from northern Angola and Congo.

14. Typhlops angolensis adolfi Sternfeld—A savanna form from eastern southern Congo and eastern Africa. T. kaimosae Loveridge is a synonym based on an individual anomaly.

15. Typhlops angolensis dubius Chabanaud—Populations from grassy highlands in Kivu, Uganda, Ituri and Ruanda-Urundi.

16. Typhlops angolensis symoensi Laurent—A form derived from *dubius* in southern Itombwe (southern Kivu).

17. Typhlops angolensis polylepis Laurent-Western mountain forest in Kivu.

18. Typhlops angolensis irsaci Laurent—Eastern mountain forest in Kivu and Ruanda.

19. Typhlops angolensis blanfordi Boulenger—Northeastern African highlands.

CHARACTERS EXAMINED ¹

1) Rows of scales at midbody. This character has long been recognized as of high diagnostic value. It is often variable within populations but this variability is generally low: 2, 4, 6 and rarely more; the odd numbers are infrequent.

In T. angolensis, a positive correlation between the altitude and number of midbody scale rows has been disclosed (Laurent, 1960).

¹ Data from the MCZ and AMNH, CNHM, USNM collections and from Laurent (1956, 1960).

The variation for all the forms examined is shown in Table 1 (frequencies given as percentages).

2) Difference between the number of scale rows at midbody level and behind the head. (See Table 2.)

3) Difference in the number of scale rows between the preanal region and the midbody region. (See Table 3.)

4) Number of scales between the prefrontal and the end of the tail. (See Table 4.)

5) Shape of prefrontal. This character has already been stressed as an obvious difference between *T. angolensis, sensu lato,* and the *punctatus-boulengeri-schmidti* complex (Laurent, 1956). In the first group it is subhexagonal; in the second, subtrapezoidal. The subhexagonal type exists also in *blanfordi, steinhausi,* and *obtusus,* all forms here considered as subspecies of *T. angolensis* or closely related to this species.

On the other hand, gierrai and tanganicanus have the subtrapezoidal form described for schmidti.

In *T. congestus*, the prefrontal is hexagonal as in *T. angolensis* but flatter (shorter) and wider. In *T. punctatus liberiensis*, a somewhat intermediate condition occurs, tending to the trapezoidal form of *punctatus*. In *rondoensis*, the form is subtrapezoidal, but less angular. It is rounded and very small in *fornasinii*.

Shape of the supraocular. An almost perfect correlation is 6)obvious between the shape of the prefrontal and the shape of the supraocular. When the prefrontal is subtrapezoidal, the supraocular is band-like and oblique, with its lateral angle inserted between the nasal and the preocular; this condition is seen in punctatus, boulengeri, usambaricus, gierrai, tanganicanus, schmidti. When it is subhexagonal, the supraocular is transversely oriented with its lateral angle inserted between the preocular and the ocular; this condition is seen in T. angolensis and all its subspecies, as in obtusus and fornasinii. T. congestus shows almost the same outline but somewhat approaching the oblique band of *punctatus*; in 2 specimens out of 56, the lateral extremity is between the nasal and the preocular. In T. punctatus liberiensis, the punctatus condition prevails, with some intermediates with the lateral end between the ocular and the preocular (the latter only on 2 sides of 18 Liberian individuals, but in 6 specimens and 2 additional sides of 10 from Ghana-a cline?).

Some exceptions concerning the location of the external end of the supraocular have been observed in *punctatus* (symmetrical in 2 specimens and asymmetrical in 2 others of 14 individuals), in

gierrai and boulengeri (asymmetrical in 4 specimens out of 25). In T. rondoensis the supraocular is oblique but more rounded, its external end in contact with the nasal.

7) Size and location of the eye. The eye is larger in punctatus than in any other form. When the eye is hidden, this condition is generally correlated with a peculiar appearance of the scales and a lacteous hue obscuring any color pattern; this seems to precede sloughing but is striking enough to have been wrongly considered as a taxonomic character. The eye is behind or partly below the ocular-preocular limit in punctatus, liberiensis, congestus, boulengeri, usambaricus, tanganicanus, schmidti, fornasinii. It is below the same limit or anterior to it in T. angolensis, and clearly before it (below the preocular) in T. rondoensis. These relations concern the superficial sutures.

8) Nasal suture. The nasal suture generally joins the nostril to the first labial border, but in the eastern populations of *congestus* it generally ends at the rostral limit. It seems that this condition becomes less frequent towards the west; exceptions (i.e. termination at the limit between rostral and first labial) have been more often remarked in specimens from central Congo. In the samples from Cameroon and in *T. punctatus liberiensis*, the "eastern" condition is sometimes seen asymmetrically, and even symmetrically in one case (*Typhlops leprosus* Taylor and Weyer).

In *T. fornasinii*, the suture may go beyond the nostril (type of *tettensis*) or even completely divide the nasal plate (type of *mossambicus*).

9) Labials touching the preocular (see Table 5). In boulengeri, the frequency of the contact of labials 1 and 2 with the preocular is high in the Congolese and Sudanese samples, and low in east African samples; an internal cline is probable. The absence of contact is effected in two ways: in gierrai, a supplementary scale comes between the labials and the preocular; in the type of kaimosae, the nasal is in contact with the ocular below the preocular, but this is an abnormal condition—as proven by the existence of sympatric specimens of adolfi which differ only by the absence of this peculiarity.

10) Shape of the contact between the labials and the preocular (or the intercalary scale in *gierrai*). The shape of this contact has often proven to be taxonomically significant. It may be straight or angular; when it is angular two labials are necessarily involved since a labial never has a concave outline.

The contact is almost always straight in *boulengeri*, usambaricus, schmidti, tanganicanus, fornasinii, steinhausi, irsaci, blanfordi. It is generally so in rondoensis and dubius.

The contact is angular in *punctatus*, gierrai, obtusus, angolensis, and symoensi. It is generally so in *liberiensis*, congestus, polylepis, and adolfi.

11) Color pattern. The coloration appears in two radically different phases which, oddly enough, rarely occur in the same populations in the former Belgian Congo, but are frequently co-existent outside this area.

One of these phases is spotted or marbled: the pigmentation is so unevenly distributed that some groups of scales are devoid of any pigment, while others are almost black. Two forms have this kind of coloration exclusively: usambaricus (but only two specimens of the latter are known to me), and the eastern populations of T. congestus.

The same pattern is frequent but not universal in *congestus* (western populations), punctatus, liberiensis and gierrai. It may occur but rarely in schmidti, rondoensis (one specimen), and bou*lengeri* (one specimen from Ujiji; I have never seen it in any of the numerous Congolese specimens examined in the past). It seems never to be present in T. angolensis and its races. Two aspects are recognizable in this marbled pattern. The belly may be marbled like the back: this is the rule in T. punctatus punctatus, and the only spotted specimen of T. boulengeri I have seen is similar. In all the other forms with marbled pattern, the belly is always immaculate. The other phase is more evenly pigmented. Each dorsal scale is partly pigmented. Sometimes, the pigment is concentrated on the sides of the scales producing a striped pattern. Sometimes, it forms a transversely elongated blotch leaving a smaller light area in front and a larger behind; this tendency seems to be frequent in the angolensis group and T. obtusus, but the number of specimens at hand does not permit any generalisation. Sometimes, the black pigment forms a horseshoe pattern on each scale, with the main light area in front; this pattern is seen in T. punctatus, T. congestus, T. boulengeri, T. schmidti, T. gierrai. Both patterns occur in rondoensis. In either case, a finely punctate appearance is the result of this distribution of pigment. Often the pigment invades the light areas and the scales then become uniformly blackish or nearly so. This happens in the eastern populations of T. angolensis and some individuals of T. punctatus and T. boulengeri.

The greater or lesser development of pigmentation has another aspect. When pigment is relatively scant, the belly is generally

BULLETIN: MUSEUM OF COMPARATIVE ZOOLOGY

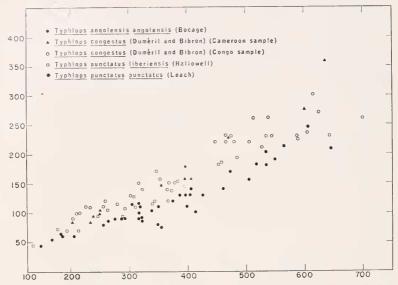


Fig. 1. Scatter diagram of the diameter of the body (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

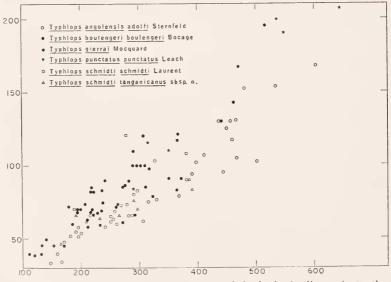


Fig. 2. Scatter diagram of the diameter of the body (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

immaculate; when it is extensive, the number of pigmented scale rows increases until all the ventral rows are affected. Generally there is less pigment ventrally so that even if the dorsal scales are entirely black, the lateral and ventral scales have a light central spot, which is larger in the ventral scales. In this case, we have a dorsoventral gradient of pigmentation. In other cases, there is a sharp difference between the dark back and the light belly, the limit being straight or irregular, lateral or ventral with a narrow light ventral band.

T. fornasinii, very different in its low longitudinal scale count, is also very different in its uniform pigmentation.

12) Ratio between the length of body and its largest diameter. This character is unfortunately affected by the physiological condition of the specimen when killed and the state of preservation. However, some species are slender while others are thick. No sexual correlation is apparent in this character. (See Table 6; Figs. 1 and 2.)

13) Ratio between the length of body and the breadth of the head. (See Table 7; Figs. 3 and 4.)

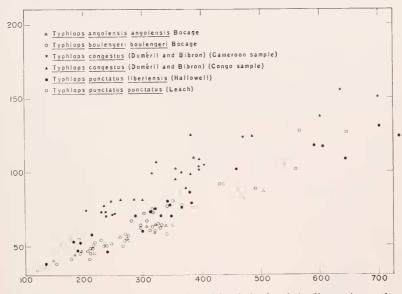


Fig. 3. Scatter diagram of the breadth of the head (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

BULLETIN: MUSEUM OF COMPARATIVE ZOOLOGY

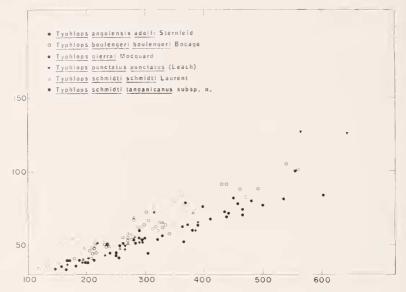


Fig. 4. Scatter diagram of the breadth of the head (ordinate, in tenths of millimeters) versus the length of the body (abscissa, in millimeters).

14) Relative breadth of the prefrontal. This character displays a large individual variability and, as such, is not very useful. The percentage values of this measurement in relation to the breadth of the head are given here but only for some samples. An interesting difference appears between congestus and liberiensis.

> Breadth of prefrontal/breadth of head (in per cent) (Modal condition in bold face)

	26-30	30-34	34-38	38-42	42-46	46-50	50-54	54-58
T. punctatus liberiensis (27) T. congestus				11	33	33	12	11
congestus (33)	3	6	6	49	33	3		
T. boulengeri (38)		3	8	13	24	26	13	13
T. gierrai (9)			22	23	55			
T. schmidti								
tanganicanus (9)				11	33	34	22	
T. rondoensis (10)			10	30	50	10		
T. angolensis subsp. (33)	3	9	18	43	15	19		

RECOGNITION OF "NON-DIMENSIONAL" SPECIES

In his outstanding revisionary study of *Dasypeltis*, Gans (1959) began his investigation by the examination of the cases of sympatric differences. No better approach to a difficult taxonomic problem can be conceived and it should be adopted by every taxonomist.

Sympatry of punctatus and congestus. From Sakbayema, Cameroon, the MCZ has four specimens of congestus and one specimen of punctatus.

The *congestus* individuals have no ventral pigmentation except some lateral encroachments of the dorsal blotches in some of them. On the contrary, the belly is pigmented except in the midventral region in the *punctatus* individual.

The following correlated differences prove that the "*punctatus*" and "*congestus*" specimens could not pertain to the same population.

	congestus	punctatus
Supraocular	nearly transverse	definitely oblique
Midbody scale rows	26-28	30
Scale rows in front	19-22	26
of anus		
Longitudinal number of	∫ 322-354 (4 ♂ ♂) } 341-382 (8 ♀ ♀	-376 (δ from another locality
scales)́ 341-382 (8 ♀ ♀	in Cameroon)
	from other local-	428 (♀)
	ities)	
Ratio length/diameter	21.8-29	33
Ratio length/breadth	38.3-43.7	53.2
of head		

Sympatry of punctatus and boulengeri. I have already recorded the coexistence of these two forms in the northern Congo (Laurent, 1956). Schmidt's data (1923) also prove that these forms are sympatric (at Poko) and thus specifically distinct; however, he confused *punctatus* with *congestus* and gave the name of *punctatus* to *boulengeri*.

The significant data are as follows:

	punctatus	boulengeri
Belly	dark or mottled	light
Size	549 - $605 \mathrm{mm}$	$139\text{-}308 \mathrm{~mm}$
Scale rows behind the head	32-34	26-28
Midbody scale rows	30-32	26-28
Shape of the contact	angular	straight
between preocular and labials		

T. punctatus and T. boulengeri are also sympatric in the Sudan. The MCZ has three specimens of T. boulengeri, but no T. punctatus from this area; however, true Sudanese punctatus exist in the collections of the British Museum (Natural History) and the Chicago Museum.

T. boulengeri has the belly nearly as pigmented as punctatus in this northern part of its range. It differs however by its lower number of midbody scale rows (28-30 instead of 30-34), and more clearly by the relations between the preocular and the upper labials. The contact is straight and with the 1st and 2nd labials in the three boulengeri specimens examined from Sudan, while it is angular and with the 2nd and 3rd labials in punctatus. The longitudinal counts of scales of eleven T. punctatus are 376-403 (3 \diamond) and 399-428 (8 \updownarrow), while the Sudanese boulengeri give lower figures: 374 (\diamond), 391-400 (2 \heartsuit).

Sympatry of congestus and steinhausi. These two forms are so obviously different that their distinctiveness has never been questioned and need not be demonstrated here. They are sympatric in Cameroon.

Sympatry of congestus and angolensis. These two Typhlops have been adequately diagnosed by Schmidt (1923) but angolensis was called by him intermedius. See also Laurent (1956).

	congestus	angolensis
Color pattern	blotches	striped (each scale
		with a yellow spot)
Scale rows behind the head	28-32	24-28
Ratio total length/diameter	19-30	26-41
Ratio total length/breadth of head	27.5-45	37-61
Nasal suture	generally	from 1st labial
	from rostral	
Longitudinal scale counts	365-410 (8 ♀ ♀)	287-364 (8 ♀ ♀)
(in females only)		

Sympatry of punctatus and steinhausi. Schmidt's data (1923) show that punctatus and angolensis are sympatric in Niangara, but it could be presumed that they are ecologically separated since punctatus is an inhabitant of savannas, while angolensis lives in the forest. While examining this material in New York I discovered that the "intermedius" specimens from Niangara are not angolensis but steinhausi.

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

	punctatus	steinhausi
Belly	pigmented	not pigmented
Scale rows behind the head	32-34	24-26
Midbody scale rows	30-32	25-26
Scale reduction between	6	1-2
midbody and vent level		
Prefrontal	trapezoidal and wide	subhexagonal and narrow
Supraocular	oblique, apex generally	transverse, apex between
	between nasal and pre- ocular	preocular and ocular
Eye	large, below ocular	smaller, below preocular
Labials touching preocular	2-3, contact angular	1-2-3, contact straight

Sympatry of boulengeri and adolfi. It was the coexistence of two entirely different "Typhlops punctatus" at Uvira, Kivu, and the Mosso region, Urundi, which induced me to question the conception of a wide-ranging and variable species called T. punctatus. In fact, this difference has been recognized repeatedly: not only did Schmidt (1923) make a distinction between the two species involved, but Bocage (1893) did also, in describing T. boulengeri, and Boulenger (1899) as well, in describing T. blanfordi. Loveridge (1942) did the same, recognizing T. blanfordi lestradei as distinct from his T. punctatus. His concept of T. punctatus in East Africa is correct in the sense that it is not a composite as I once believed. Except for two montane specimens apparently referable to a new form, his T. punctatus is simply T. boulengeri. In this he follows Schmidt. However, his western "punctatus" material is a mixture of several species.

The characters which prove that *boulengeri* and *adolfi* are specifically distinct are as follows:

	boulengeri	a dol f i
Color	lighter	darker
Prefrontal	wide, subtrapezoidal	narrower, subhexagonal
Supraocular	oblique, apex touching	transverse, apex touching
	the nasal	the ocular
Eye	behind the posterior	below or before the
	border of preocular	posterior border of pre- ocular
Contact between	straight, predominantly	generally angular, with
preocular and	with 2nd labial, often	2nd and 3rd labials
upper labials	also with 1st or 3rd	
	labial	
Midbody scale rows	28, rarely 30	30 or 32, rarely 28
Ratio length/diameter	24-39	25.5-50
Ratio breadth of	0.92-1.33	1.22 - 1.66
head/breadth of tail		
Maximum size	$50~{ m cm}$	$62~\mathrm{cm}$

BULLETIN: MUSEUM OF COMPARATIVE ZOOLOGY

Sympatry of boulengeri and schmidti. T. schmidti is a Katangese species which has been confused with boulengeri and adolfi under the name of "punctatus" (de Witte 1933b, 1953). The complete disentangling of this material is yet to be accomplished, and at the present time the respective distributions of the three species in this area are not known in detail.

At Sandoa, however, the three forms are known to occur together.

The significant differences are the following:

	boulengeri	schmidti
Belly	generally pigmented,	generally not
	however slightly	pigmented
Midbody scale rows	28 (rarely 30,	22-24 (rarely 26)
	sometimes 26)	
3rd labial	not often in contact with	nearly always in
	preocular (25% of sides in	contact with
	Congo specimens)	preocular
Reduction in the number	- · ·	1
of scale rows		
at midbody	rarely more than one	rarely less than two
at anal region	usually more than two	generally two
Longitudinal counts		Bonchard Child
රි රි	351-393 (7 spec.)	317-325 (2 spec.)
Q Q	384-400 (8 spec.)	370 (1 spec.)

Sympatry of gierrai and usambaricus. From Amani, Usambara Mountains, the MCZ has a small series of *T. gierrai* and two additional spotted specimens which appear to represent an unrecognized form (both forms are spotted). Loveridge considered gierrai as a race of "punctatus" (understanding by this what I here consider boulengeri). The specimens here described as usambaricus were recorded by Loveridge as intermediates between "punctatus" and gierrai. They are clearly different from gierrai and cannot belong to the same population.

	gierrai	usambaricus
Scales outside spots Contact between pre- ocular and labials	black bordered inferior part of preocular separated, forming an angular contact with 2nd and 3rd labials	unpigmented preocular undivided in straight contact with 2nd and 3rd labials
Scale rows in front of the vent	24-26 (23 in one specimen)	22
Eye	under the posterior border of the preocular	behind the posterior border of the preocular

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

	gierrai	usambaricus
Longitudinal count	398-464	344-390
of scales		
Ratio length/diameter	31,2-44	27-31.1
Ratio length/width	42.5 - 58.4	38.4 - 42.2
of head		

Conclusions. From the foregoing it must be concluded that eight specific gaps, proved by sympatric relationships, are evident in the "Typhlops punctatus" complex.

ALLOPATRIC RELATIONSHIPS

The populations of western Africa (Liberia to Ghana). Notwithstanding the number of names which have been based on specimens from this region, there are no apparent grounds for a taxonomic splitting of these populations of *Typhlops*. The characters bridge the gap between true *punctatus* and the Cameroon populations (congestus). The color pattern is variable in the three groups, with two phases: the "punctatus" phase with each scale bicolored (the amount of black pigment decreasing from the back to the sides or to the belly), and the "blotched" phase.



Map 1. Distribution of species of the *Typhlops punctatus* group in West Africa.

In the savanna populations the ventral pigmentation is strongly developed, i.e. nearly all the ventral scales are partly pigmented, and the blotched phase has spots on the belly. In the two other samples the belly is generally devoid of any pigment except for some punctating or spots on the sides, which may be rather frequent; sometimes the light part of the belly is narrow, but only one

specimen from Ghana (Somenya, MCZ 55318) has black spots on most of the ventral scales.

The number of midbody scale rows approaches the *congestus* figures; they are 26 to 28, rarely 30, instead of 30-32 for *punctatus*. The longitudinal scale counts are intermediate, but nearer to *punctatus*.

	punctatus	Liberia-Ghana	congestus (Cameroon only)
88	376-403 (n=3)	339-385 (n=10)	322-354 (n=6)
	(m=387)	(m = 363.2)	(m=339.17)
♀ ♀	399-428 (n=8)	371-435 (n=9)	341-382 (n=10)
	(m=423)	(m=400.78)	(m=364.83)

The shape of the prefrontal is also intermediate. The shape of the supraocular is generally similar to that of *punctatus* but with a definite tendency in eastern populations to the *congestus* condition, i.e. the lateral apex is between the preocular and the ocular in 7 per cent of the cases in Liberia but in 68 per cent in Ghana.

The nasal suture arises from the rostral with a frequency of 22 per cent; such a condition has never been recorded in *punctatus*, but occurs in *congestus*, rarely in Cameroon populations, as a general rule in eastern Congo samples.

The contact of preocular with labials is angular in the three groups with only one symmetrical exception in a Ghana specimen (Somenya, MCZ 55318) and one asymmetric exception in a Cameroon specimen (Lolodorf, MCZ 9241).

The scatter diagram for the relative thickness of the body shows that the Liberia group resembles *punctatus* more than *congestus*; for the relative width of the head, the Liberia group is intermediate.

The relative breadth of the prefrontal, ranging from 41.1 to 55.6 per cent of width of the head (m=47.78), is clearly greater than that of *congestus*, which ranges from 28.2 to 42.9 per cent (m=38.98) but does not differ from that of *punctatus* with a range of 40 to 56.1 (m=46.38).

The characters checked support equally a conspecific relationship with *punctatus* or with *congestus*, or even with both. However, we already know that *congestus* can be sympatric with *punctatus* in at least one locality of Cameroon. Moreover, we have strong evidence that the Congolese populations of *congestus* are not connected to *punctatus* by hybrid populations although they are still not known to be sympatric in any locality; the differences appear too clear-cut in view of the shortness of the distance between the least distant localities (Poko and Akenge).

It is, of course, still possible that *congestus* is subspecifically related to the Liberia populations and by way of these with *punc-tatus*. But as there exists a distributional gap between the western forest populations and those of Cameroon, we are permitted to postulate that they do not belong to the same species.

The data for the Ghana specimens suggest a short cline between the southern forest populations and the northern savanna ones. Thus, the conditions appear to warrant the recognition of subspecific relationships between these populations.

Western and eastern populations of T. congestus. The spotted forest Typhlops of Congo (ex Belgian Congo) have been referred by Schmidt (1923) and Laurent (1956) to T. congestus. However, they appear to differ from the Cameroon samples, as shown below.

	Cameroon	Congo					
Color pattern	spotted and punctate phase	spotted phase only					
Nasal suture	generally from 1st labial	generally from the rostral					
Longitudinal counts							
of scales							
8 8	322 - 354 (6)	331-378 (12)					
Q Q	341-382 (10)	381-404 (5)					
Relative thickness of	somewhat larger in th	ne Congo specimens					
body and relative	(see scatter	(see scatter diagram)					
breadth of head							

The populations from Cameroon and eastern Congo are thus fairly different and could perhaps be treated as subspecies; however, the populations of western Congo, which are poorly known, are likely to provide a smooth clinal transition. In consequence, no subspecific distinction is here proposed.

The Usambara Mountains population of T. boulengeri. Two specimens from Amani (MCZ 23099 and 38699) differ from the sympatric T. gierrai (see above) and from the allopatric boulengeri. I have seen more than 130 specimens of boulengeri from the Congo and 25 additional specimens in the MCZ collection; to these figures we may add the 15 specimens examined by Schmidt (1923). One, from Ujiji (MCZ 30037) has a spotted pattern on the belly as well as on the back (a pattern observed elsewhere only in T. punctatus). The two Amani individuals, however, are only spotted on the back. Since this pattern is never encountered in typical T. boulengeri, it may be assumed that it is characteristic of a montane population which is recognizable as a race.

Typical populations of T. schmidti compared with eastern populations. The material referred by Loveridge to T. tettensis (1955,

1956) is so strikingly like *T. schmidti* that I believed, after a first examination, that *schmidti* was simply a synonym of *tettensis*. Some differences exist, however, and justify a subspecific discrimination, pending the ever-possible discovery of a connecting cline. The name of the species must be *schmidti*, since *tettensis* is an entirely different species as explained below:

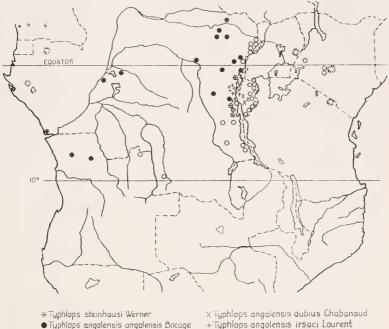
	schmidti	eastern sample (Liwale, Kilwa)
Midbody scale rows	22 to 26	21 to 24
	(22 in 32% of specimens, 24 in 63%, 26 in 5%)	(21 in 12%, 22 in 44%, 24 in 44%)
Reduction of scale rows	4, sometimes 2, rarely 0	2 or 0, rarely 3
from front part of		
body to midbody		
Longitudinal counts 8 8	317-325(2)	352-376(4)
Q Q	370	400-425(6)
Belly	not pigmented	slightly pigmented
Ratio length/diameter	23-42.7 (m=33.58)	29-47 (m=37.82)
Ratio length/width of	40.6-52.7 (m=48.33)	47-64 (m=54.57)
head		

Allopatric relations of T. angolensis. The subspecific differentiation of T. angolensis in the territory of the former Belgian Congo has been described by me (1956, 1960). Loveridge (1942) has correctly pointed out the relationships between angolensis mountain populations of Kivu, Ruanda and Uganda (which he called *lestradei*), and T. blanfordi. This form is related to dubius (= lestradei) and to adolfi.

The color pattern is similar, but with a mid-belly light zone in some individuals. As I know only two specimens of *blanfordi*, I cannot tell what the frequency of this character is. The difference from *adolfi* is that the contact between the preocular and the labials is straight and not angular.

The longitudinal count of scales is 347-392 in *blanfordi* (2 & &), 411-573 in *dubius* (15 specimens which are unsexed because they were eviscerated); these counts are poorly known in the other races, but some indications suggest an altitudinal cline, since one \bigcirc of *irsaci* has 520 scales and 2 && have 425 and 485, while 8 $\bigcirc \bigcirc$ of the typical lowland form have 287 to 364 scales and 12 &&&have 281 to 371 scales.

T. kaimosae differs from adolfi in the absence of any contact between the preocular and the labials (nasal and ocular contiguous below the preocular); but this peculiarity is not shared by two other specimens from Kenya, which are referable to adolfi, the



OTyphlops angolensis adolfi Sternfeld Tuphlops angolensis polulepis Laurent Tuphlops angolensis sympensi Laurent

Map 2. Distribution of species of the Typhlops angolensis group in the region of the Congo.

distribution of which is therefore considerably extended towards the east.

Some relations with southern and southeastern forms like obtusus, fornasinii, bibroni and even rondoensis are probable but they are not close enough to warrant any taxonomic recognition.

Relationships between T. angolensis and T. steinhausi. The seven specimens seen of T. steinhausi agree with T. angolensis in many characters: number of scale rows, color pattern, shape and connections of prefrontal and supraocular, position of eye. T. steinhausi differs from T. angolensis by the relations of the preocular and the labials: the contact is straight as it is in some highland populations of T. angolensis (dubius and irsaci), but with three labials (1st to 3rd) as it is in some individuals of T. boulengeri. The longitudinal counts of T. steinhausi are considerably higher than in angolensis (typical form): 402 to 425 instead of 281

to 371. Lastly, T. steinhausi is more slender. The ratio between the total length and the diameter varies from 39.8 to 50. 3 (n=7) (m=43.10), while in the lowland forest T. angolensis, the figures are 26.7 to 40.5 (n=33) (m=33.39). Before seeing the collections of the American Museum of Natural History, I was prepared to treat steinhausi as a subspecies of T. angolensis though it appeared as the most sharply differentiated of all the races of this species. It was plausible as a Cameroon subspecies. I was surprised to discover at the American Museum of Natural History that this form is also present in the northern part of the eastern Congo.¹ Schmidt's series of T. intermedius (1923) includes two specimens of T. steinhausi from Niangara. This is a quite unexpected extension of range and very unlikely for a subspecies of T. angolensis. Sympatry with angolensis is not yet proven, but such a proximity of clearly different populations is hardly compatible with a subspecific status when no obvious barrier is involved in the picture.

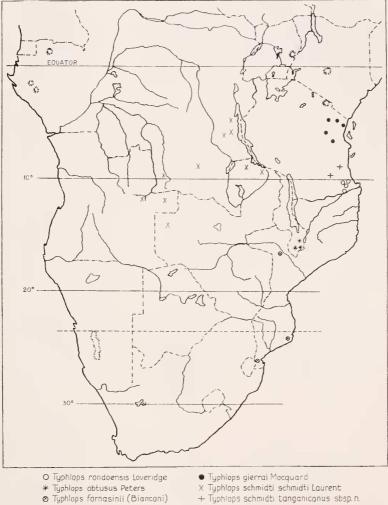
The relationships of the southeastern forms. The allopatric forms which Loveridge (1942, 1955, 1956) considered as races of a single species and called T. t. tettensis, T. t. rondoensis, and T. t. obtusus, are not closely related, in my opinion.

Tettensis Loveridge is widely different from tettensis Peters, and is a race of T. schmidti which deserves a new name; tanganicanus subsp. n., T. tettensis Peters, and T. mossambicus Peters are synonyms of T. fornasinii Bianconi.

The differences between these forms are such that it can hardly be doubted they are full species, with the possible exception of rondoensis. It could be argued that rondoensis is not very different from tanganicanus, but it is obvious that tanganicanus is more closely related to schmidti which is geographically more distant. The location of the eye which is fairly constant in the species of the group is different in rondoensis, as well as the more rounded shape of the prefrontal and the supraocular; this suggests that rondoensis comes from a much older phylogenetic dichotomy than the tanganicanus-schmidti divergence.

The differences between these four forms are tabulated on page 410 (data from the MCZ collection, plus Peters' data from "Reise nach Mossambique").

¹ It is very likely that the Museum of Central Africa has many specimens of this species too.



- ★ Typhlops obtusus Peters
 ⊘ Typhlops fornasinii (Bianconi)

Map 3. Distribution of species of the Typhlops punctatus group in southeastern Africa.

fornasinii (=tettensis Peters)	Mozambique lowlands	22-24-26	-2-0-2	252-272 (9)	small, rounded		transverse, apex in contact with ocular	below preocular	straight, with	2nd labial only					pigmented	(unicolor)	23 - 36.9	(m=30.77)	33-48.3	(m=40.12)
obtusus	Nyasa highlands	24 (rarely 25)	2-4	417-484(5)	subhexagonal		transverse, apex in	invisible	angular, with	2nd and 3rd	labials (2nd	only, 3rd only or 3rd & 4th	in some sn	fide Loveridge)	non pigmented		51.1-61.1	(m=54.56)	70-85.5	(m=77.18)
rondoensis	Rondo Plateau	24 (rarely 22)	0-2	314-353 (10)	subtrapezoidal	but more rounded	act with nasal	below preocular	straight, with 2nd	labial only					non pigmented		28.8-39 (m=39.83)		41.2-57 (m=50.13)	
tanganicanus (=tettensis Loveridge not Peters)	lowlands of south- eastern Tanganvika	22-24 (rarely 21)	0-2 (rarely 3)	352-425(10)	subtrapezoidal		oblique, apex in contact with nasal	below ocular	straight, with 2nd and	3rd labials, rarely	with 2nd only				slightly pigmented		29-47 (m=37.82)		$46-64 \ (m=53.73)$	
	Range	Midbody scale rows	Midbody reduction of scale rows	Longitudinal counts	Prefrontal		Supraocular	Eye	Contact between	preocular and labial					Belly		Ratio length/diameter		Ratio length/breadth	of head

410 BULLETIN: MUSEUM OF COMPARATIVE ZOOLOGY

SYSTEMATIC ACCOUNT

TYPHLOPS PUNCTATUS PUNCTATUS (Leach)

- 1819 Acontias punctatus Leach in Bowdich, Mission . . . Ashantee, app., p. 493, "Fantee," i.e. Fanti, Ashanti, Ghana.
- 1844 Typhlops cschrichti Schlegel, Abbild. Amph., p. 37, pl. XXXII, figs. 13-16, Ghana.
- 1893 Typhlops punctatus: Boulenger (part)¹, Cat. Snakes Brit. Mus., vol. 1, p. 42, Aa (Fantee, Gambia, Monbuttu, Lado) Ab (Monbuttu).
- 1923 Typhlops congestus: Schmidt (part, non Duméril and Bibron), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 48, Niangara, Poko.

Description. Dark brown above, each seale with a small yellowish spot; each ventral scale yellowish in the center and brown on the borders, or with scattered irregular yellow blotches above and below. Scale rows: 28-30-22 to 34-33-26. Number of scales between the prefrontal and the tip of the tail: 376-403 (3 & &), 399-428 (8 & &)). Prefrontal subtrapezoidal, broad. Supraocular oblique, its side apex generally between the nasal and the preocular. Eye large, behind the posterior border of the ocular. Nasal suture arising from the 1st labial. Preocular wedge-shaped below, between the 2nd and 3rd upper labials. Diameter of body 35 to 42 times, and breadth of head 43 to 54 times, in the total length. Size large, up to 650 mm and probably more.

Distribution. From Uganda west to Senegal, through Sudan and northern Congo. The greatest part of the records of T. punctatus from the savanna region are probably really referable to this form.

1 Some words of explanation seem necessary concerning the usage of the word "part" and its varying position in these citations.

a) When the name of the species is followed directly by the name of an author not the original describer of the species and the author's name is then followed by "part" between parentheses, it means that part of the material referred to in the citation was correctly identified by the author, but that another part was not, and that this citation is for that part of the material which was correctly identified.

Example: Typhlops congestus: Schmidt (part) listed in the synonymy of Typhlops congestus (Duméril and Bibron).

(gestus (Dumeniand Bioron). b) When the name of the species is followed by the name of an author not the original describer and then is followed by "part, non name of the original author of the species" between parentheses, it means that part of the material referred to was wrongly identified by the author, but also that another part of this material was not, and that this eitation is for that part of the material which was wrongly identified.

Example: Typhlops congestus: Schmidt (part, non Duméril and Bibron) listed in the synonymy of Typhlops punctatus (Leach).

c) When the name of the species is immediately followed by "non name of the original author" between parentheses, then by the name of an author not the original describer, and finally by "part," between parentheses, it means that the whole material was wrongly identified and that the material is also composite; in other words, the several forms were confused and none actually belonged to the species to which they were referred.

Example: 1919 Typhlops punctatus (non Leach): Boulenger (part) listed in the synonymy of Typhlops congestus (Duméril and Bibron).

Specimens examined. Ghana. USNM 56290. Cameroon. Sakbayene: MCZ 22828. Boli: MCZ 44101. Northern Congo. Niangara: AMNH 11669-70. Poko: AMNH 11671-72. Ekibondo: MCZ 44279. Tchad. Fort Archambault: USNM 137761. Fort Crampel: MCZ 55415. Nigeria. Marama: USNM 125681. Wushishi: CNHM 42563. Southern Sudan. Lipangu: CNHM 58314. Uganda. Kaliro, Busoga: AMNH 63768.

TYPHLOPS PUNCTATUS LIBERIENSIS (Hallowell)

- 1848 Onychocephalus liberiensis Hallowell, Proc. Acad. Nat. Sci. Phila., 1848, p. 59, Liberia.
- 1848 Onychocephalus nigro-lineatus Hallowell, Proc. Acad. Nat. Sci. Phila., 1848, p. 60, Liberia.
- 1864 Typhlops liberiensis var. intermedia Jan, Icon. Gen. Ophid., p. 24, and vol. 1, livr. 5, pl. V, fig. 2, pl. VI, fig. 2, Liberia.
- 1864 Typhlops kraussi Jan, Icon. Gen. Ophid., p. 26 and vol. 1, livr. 3, pl. VI, fig. 2, Ghana.
- 1864 Typhlops lineolatus Jan, Icon. Gen. Ophid., p. 24 and vol. 1, livr. 9, pl. I, fig. 4, Sierra Leone.
- 1864 Typhlops hallowellii Jan, Icon. Gen. Ophid., p. 29 and vol. 1, livr. 4, pl. IV, fig. 6, pl. V, fig. 6, Ghana.
- 1893 Typhlops punctatus: Boulenger (part, not of Leach), Cat. Snakes, Brit. Mus., vol. 1, p. 42, Ac (West Africa), Bd (Gambia, Oil River), Bs (Accra, Ghana), Be (Ashanti, Sierra Leone).
- 1920 Typhlops milleti Chabanaud, Bull. Mus. Hist. Nat. Paris, vol. 26, p. 463, Togo.
- 1940 Typhlops punctatus punctatus (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Ganta, Liberia.
- 1958 Typhlops leprosus Taylor and Weyer, Univ. Kansas Sci. Bull., vol. 38, p. 1204, Harbel, Liberia.

Description. Dark brown above, each seale with a small yellowish spot, generally uniform yellowish below, sometimes with scattered black points or with brown bordered scales on the sides of the belly, very rarely with all the scales brown bordered as in the typical form. The yellow spots of the dorsal scales can coalesce into longitudinal lines separated by black streaks. A spotted pattern is frequent, but only on the back: black with yellow blotches, or yellow with black blotches. Scale rows: 26-24-20 to 31-30-24. Number of scales between the prefrontal and the tip of the tail: 339-385 (11 $\delta \delta$), 371-435 (14 $\varphi \varphi$). Prefrontal generally somewhat shorter than in *punctatus*. Supraocular generally as in *punctatus* in western populations, but its apex is more often than not between the ocular and the preocular in the eastern populations (Ghana). Eye as in *punctatus*. Nasal suture arising from the 1st

labial, sometimes from the rostral. Preocular generally wedge shaped below, in contact with the 2nd and 3rd labials, very rarely with the 1st and 2nd labials or the 2nd only. Diameter of body 22 to 40 times, width of head 33 to 60 times, in the total length. Size very large, up to 800 mm.

Distribution. Rain forest region and "galleries" from Ghana west to Gambia.

Specimens examined. Liberia. Bakratown: MCZ 22490-91. Gbanga: MCZ 22492-96, 51465-66. Ganta: MCZ 43182-87. Harbel, Firestone Plantation: CNHM 58039-41. Mt. Coffee: USNM 24138, 24173. Ghana. CNHM 53636. Achimota School: MCZ 53653. Akropong: MCZ 53651. Iafo forest: MCZ 49075-76. Krobo: MCZ 55315-19. Legon Hill: MCZ 53652.

TYPHLOPS CONGESTUS (Duméril and Bibron)

- 1844 Onychocephalus congestus Duméril and Bibron, Herpét, Génér., vol.
 6, p. 334, no locality.
- 1845 Onychophis barrowii Gray, Cat. Liz. Brit. Mus., p. 133, no locality.
- 1893 Typhlops punctatus: Boulenger (part, not of Leach), Cat. Snakes Brit. Mus., vol. 1, p. 42, Bb (Cameroon), Bc (Old Calabar), Bd (Old Calabar), Be (Fernando Po).
- 1919 Typhlops punctatus (non Leach): Boulenger (part), Rev. Zool. Afr., vol. 7, p. 18, Moera, northeastern Congo.
- 1923 Typhlops congestus: Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 48, Akenge, Medje, Niapu, northwestern Congo.
- 1930 Typhlops punctatus (non Leach): Barbour and Loveridge, in Strong's "African Republic of Liberia and the Belgian Congo," vol. 2, p. 786, Irumu, northeastern Congo.
- 1933 Typhlops punctatus (non Leach): Witte (part), Ann. Mus. Congo, Zool. (1) vol. 3, p. 82, Djamba, northern Congo.
- 1935 *Typhlops congestus:* Pitman, Uganda Jour., vol. 3, p. 142, pl. I, fig. 4, Budongo Forest, Bugoma Forest, Uganda.
- 1940 Typhlops punctatus punctatus (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Metet, Cameroon; Fataki, northeastern Congo.
- 1956 Typhlops congestus: Laurent, Ann. Mus. Congo, in octavo, Zool., vol. 48, p. 53, figs. 1-2, 11, pl. VII, fig. 1, Meshe, Walikale Road, Djamba, Lubongola, "Bukavu" (in error), eastern and northeastern Congo, p. 348, Hombo, eastern Congo.
- 1960 Typhlops congestus: Laurent, Ann. Mus. Congo, in octavo, Zool., vol. 84, p. 9, Irangi and between Irangi and Hombo, eastern Congo.

Description. Color pattern as in liberiensis, but only spotted phase in eastern populations. Scale rows: 28-26-19 to 30-28-22. Number of scales between the prefrontal and the tip of the tail: 322-378 (18 δ δ), 341-410 (15 φ φ) (numbers increasing from west to east). Prefrontal subhexagonal but very broad and flat. Supraocular transverse, its apex generally between the preocular and the ocular. Eye behind the anterior border of the ocular, rarely below it. Nasal suture arising from the 1st labial (west), or from the rostral (east). Preocular as in *liberiensis*, in contact with the 2nd and 3rd labials, sometimes in straight contact with them. Diameter of body 17 to 30 times, width of head 27 to 47 times, in the total length. Size large, up to 700 mm.

Distribution. African rain forest from Old Calabar to Lower Congo, east to Kivu and Uganda.

Specimens examined. Cameroon. CNHM 58943. Kribi: MCZ 7843, 7860. Kribi River: CNHM 4035. Lolodorf: MCZ 9238-41. Metet: MCZ 13215, 13239. Sakbayeme: MCZ 14983-84, 22826-28. Northeastern Congo. Irumu, Ituri: MCZ 26652. Fataki, between Irumu and Beni, Ituri: AMNH 51938. Medje, Uele: AMNH 11646-47. Akenge, Uele: AMNH 11648-63. Niapu, Uele: AMNH 11664-65. Eastern Congo. Hombo, Walikale Region, Kivu: MCZ 57458. Lower Congo. Leopoldville: USNM 20798. Western Congo. Okouma: USNM 62227.

Typhlops boulengeri boulengeri Bocage

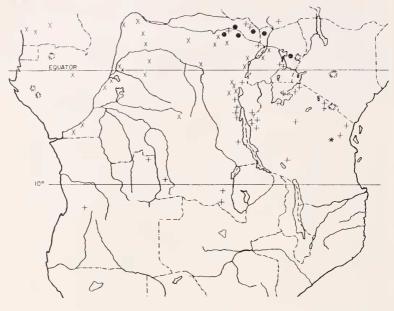
- 1893 Typhlops boulengeri Bocage, Jorn. Sci. Lisboa, (2) vol. 3, p. 117, Quindumbo, Angola.
- 1893 Typhlops punctatus: Boulenger (part, non Leach), Cat. Snakes Brit. Mus., vol. 1, p. 42, Ba (Angola, Mombuttu).
- 1910 Typhlops tornieri Sternfeld, Mitt. Zool. Mus. Berlin, vol. 5, p. 69, Kilimandjaro Mt., Tanganyika.
- 1923 Typhlops punctatus: Schmidt (non Leach), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 45, pl. I, fig. 1. Faradje, Garamba, Poko, northeastern Congo.
- 1933 Typhlops punctatus: Witte (part, not of Leach), Ann. Mus. Congo Zool., (1) vol. 3, p. 82, records mixed with T. angolensis adolf.
- 1933 Typhlops boulengeri: Witte, Ann. Mus. Congo Zool., (1) vol. 3, p. 82, Lukafu, Katanga.
- 1933 Typhlops punctatus punctatus: Loveridge (non Leach), Bull. Mus. Comp. Zool., vol. 74, p. 213, Ujiji, Mwanza, Ukerewe Id. (Tanganyika), Jinja, Mabira Forest (Uganda).
- 1935 Typhlops punctatus punctatus: Pitman, Uganda Journ., vol. 3, p. 141, pl. I, fig. 3, diverse localities from Uganda.
- 1940 Typhlops punctatus punctatus (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Harar, Ethiopia.

- 1942 Typhlops punctatus punctatus: Loveridge (non Leach), Bull. Mus. Comp. Zool., vol. 91, p. 255, Mabira Forest (Uganda), Magrotte Mtns. (Tanganyika).
- 1956 Typhlops boulengeri: Laurent, Ann. Mus. Congo., Zool., in octavo, vol. 48, p. 68, figs. 6-7, 11, pl. VIII, fig. 3, Magera, Kiharo (Urundi), Uvira, Rugari, Albertville (eastern Congo).
- 1960 Typhlops boulengeri: Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 18, Mahagi (northeastern Congo), Luberizi, Kagando, Runingo, Uvira, Kitutu, Makobola (eastern Congo).

Description. Brown above (generally less dark than in punctatus), each scale with a small yellowish spot, each ventral scale vellowish in the center and brown on the borders, with a general shading off from back to belly, some midventral scales sometimes entirely vellowish, forming light scattered spots or an irregular light area. Very rarely, a marbled pattern above and below (one single specimen from Ujiji). Scale rows: 26-24-21 to 32-30-26. Number of scales between the prefrontal and the tip of the tail: 343-401 (343-393 & &, 351-401 9 9). Prefrontal broad, subtrapezoidal. Supraocular oblique, its apex generally between the nasal and the preocular. Eye behind the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular in straight contact with the upper labials, often with the 2nd labial only (Congolese populations), less often with the 2nd and 3rd labials (eastern populations), sometimes with the 1st and 2nd labials, rarely with 1st, 2nd and 3rd labials. Diameter of body 24 to 39 times, width of head 29 to 59 times, in the total length. Size moderate, up to 500 mm in Congo and Sudan, to 560 mm in East Africa.

Distribution. Savannas of tropical Africa, from Angola east to Tanganyika, north to Sudan, west to Senegal.

Specimens examined. Cameroon. 3 km E of Kribi: MCZ 44238. Northeastern Congo. Faradje, Ituri: AMNH 11609-11, 11618. Garamba, Ituri: AMNH 11612, 11614-17. Poko, Uele: AMNH 11621-22. Eastern Congo. Luberizi, Kivu: MCZ 57457. Sudan. Kagelu: MCZ 45261. Katire: MCZ 53321-22. Ethiopia. Harar: AMNH 20339. Uganda. Jinja: MCZ 30042. Mabira Forest: MCZ 30040-41, 48059-60. Tanganyika. Ujiji: MCZ 30037. Mwanza: MCZ 30038. Ukerewe Id.: MCZ 30039. Kibonoto, Kilimanjaro: MCZ 38684. Magrotto Mtns.: MCZ 48061-65. Senheke: MCZ 49507-08. Lake Rukwa: MCZ 54586. Kasulo: MCZ 54651 Ikiju-Musoma: MCZ 54808. Majita-Musoma: MCZ 54809. Kigoma: MCZ 54810. Handeni-Yamota: MCZ 54811. BULLETIN: MUSEUM OF COMPARATIVE ZOOLOGY



Typhlops punctatus punctatus(Leach)
 X Typhlops congestus (Duméril et Bibron)

+ Typhlops boulengeri boulengeri Bocage * Typhlops boulengeri usambaricus sbsp n.

Map 4. Distribution of species of the Typhlops punctatus group in central Africa.

TYPHLOPS BOULENGERI USAMBARICUS subsp.n.

1928 "Typhlops intermediate between punctatus and gierrai," Barbour and Loveridge, Mem. Mus. Comp. Zool., vol. 50, p. 106, Amani, Usambara Mountains, Tanganyika.

Holotype. MCZ 38699, Amani, Usambara Mtns. (leg. R. E. Moreau 1935).

Paratype. MCZ 23093, same origin (leg. A. Loveridge 1926).

Diagnosis. Mountain subspecies of T. boulengeri, differing from it by its color pattern, which is marbled with yellow belly as in T. congestus.

Numerical characters

ivenierear characters										
Scale rows	Labial in contact	Long.count	Ratio length/ $$	Ratio length/						
	with preocular	of scales	diameter	width of head						
Holetype 28-26-22	2-3	344	27.5	42.2						
Paratype 29-28-22	2-3	390	31.1	38.4						

Size. Holotype: 380 mm; Paratype: 288 mm.

Distribution. Known only from Amani, Usambara Mountains. Remarks. The following records may be partly referable to usambaricus, partly to gierrai Mocquard.

- 1892 Typhlops eschrichti (non Schlegel): Matschie, Sitzb. Ges. Naturf. Freunde, Berlin, p. 110, Derema, Usambara Mountains.
- 1896 Typhlops punctatus (non Leach): Tornier (part), Die Kriechthiere Deutsch Ost-Afrikas, p. 66, Bulba, Usambara Mts., Tanga.
- 1913 Typhlops punctatus: Werner, Denkschr. Akad. Wiss. Wien, vol. 88, p. 717, Amani.

TYPHLOPS GIERRAI Mocquard

- 1897 Typhlops gierrai Mocquard, Bull. Mus. Hist. Nat. Paris, vol. 3, p. 122, Tanga, Tanganyika.
- 1928 Typhlops punctatus gierrai: Barbour and Loveridge, Mem. Mus. Comp. Zool., vol. 50, p. 106, Amani, Bagilo, Mt. Lutindi, Mlalo, Tanganyika.

Description. Dorsal scales yellowish in the center, bordered with black, ventral scales yellowish without any pigmentation. In some specimens, black dorsal blotches in which the scales are entirely black. Scale rows: 26-26-23 to 30-30-26. Number of scales between the prefrontal and the tip of the tail: 398-430 (5 & &), 439-464 (2 & &)). Prefrontal broad and subtrapezoidal. Supraocular generally oblique, its apex between the nasal and the preocular (rarely between the preocular and the ocular). Eye below the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular separated from the labials by a small scale wedged between the 2nd and 3rd labials. Diameter of body 31 to 44 times, width of head 42 to 59 times, in the total length. Size small, up to 380 mm.

Distribution. Mountain forests in Usambara and Uluguru Mountains, Tanganyika.

Specimens examined. Tanganyika. Amani: MCZ 23086-90. Mlalo: MCZ 23473. Mt. Lutindi: MCZ 23091. Bagilo: MCZ 23084.

Typhlops schmidti schmidti Laurent

- 1953 Typhlops boulengeri: Witte (part, non Bocage), Explor. Parc. Nat. Upemba, vol. 6, p. 138, Kamina, Katanga.
- 1953 Typhlops punctatus punctatus (non Leach): Witte (part), Explor. Parc. Nat. Upemba, vol. 6, p. 139, Lukuga, Katanga.
- 1956 Typhlops schmidti Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 71, figs. 9–11, pl. VIII, fig. 4, Nyunzu, Kabila, Lukuga, Sandoa, Kamina, Katanga.

Description. Dorsal scales yellowish in the center, brown on the borders; ventral scales without pigment, except sometimes the lateroventral ones. Spotted pattern in certain individuals. Scale rows: 24-22-20 to 28-26-22. Number of scales between the prefrontal and the tip of the tail: 317-325 (2 & &), 344-370 (2 & & &). Prefrontal broad and subtrapezoidal. Supraocular oblique, its apex between the nasal and the preocular. Eye behind the posterior border of the preocular. Nasal suture arising from the 1st labial. Preocular in straight contact with the 2nd and 3rd labials, rarely with the 2nd only. Diameter of body 23 to 43 times, width of head 40 to 53 times, in the total length. Size small, up to 380 mm.

Distribution. Katanga, northeastern Angola, North Rhodesia. Specimens examined. Katanga. Sandoa: MCZ 57462. North Rhodesia. Abercorn: MCZ 55479-80. Edge of Liuwa Plain: CNHM 133036.

TYPHLOPS SCHMIDTI TANGANICANUS subsp.n.

- 1951 Typhlops tettensis ?obtusus: Loveridge (non Peters), Bull. Mus. Comp. Zool., vol. 106, p. 186, Liwale, Tanganyika.
- 1955 Typhlops tettensis tettensis: Loveridge (non Peters), Jour. E. Afr. Nat. Hist. Soc., vol. 22, p. 181, Liwale, Tanganyika.
- 1956 Typhlops tettensis tettensis: Loveridge (non Peters), Tanganyika Notes and Records, 1956, no. 43, p. 10, Kilwa, Tanganyika.
- 1959 Typhlops tettensis tettensis (non Peters): Loveridge (part), Proc. Zool. Soc. London, vol. 133, p. 37, Liwale, Tanganyika.

Holotype. 1 \circ (MCZ 57439), Liwale, Tanganyika, 11-III-26-IV 1958 (leg. Ionides).

Paratypes. 1 & (MCZ 50066) same locality, 24-I-1948 (Ionides); 1 \circ (MCZ 55471), same locality, without date (Ionides); 2 \circ \circ , 1 \circ (MCZ 55623-25), same locality, 17-II-1951-I-1952 (Ionides); 1 \circ , 1 specimen the sex of which could not be determined (MCZ 57437-38), same locality (Ionides); 1 \circ (MCZ 54509), Kilwa, Tanganyika, IV-1954 (Ionides); 1 \circ (CNHM 81011), Liwale, Tanganyika (Ionides).

Diagnosis. Differing from *schmidti* by a higher longitudinal scale count (352-376 instead of 317-325 in males, 400-425 instead of 344-370 in females) and by the fact that the ventral scales are more or less pigmented.

Variation. Scale rows: 24-21-19 to 24-24-20. Preocular in straight contact with the 2nd and 3rd labials, rarely with the

2nd only.¹ Diameter of body 29 to 47 times, width of head 46 to 64 times, in the total length. Size small, up to 390 mm.

Distribution. Southeastern Tanganyika.

TYPHLOPS RONDOENSIS Loveridge

- 1942 Typhlops tettensis rondocnsis Loveridge, Bull. Mus. Comp. Zool., vol. 91, p. 256, Nchingidi, Rondo Plateau, southeastern Tanganyika.
- 1956 Typhlops tettensis rondoensis Loveridge, Tanganyika Notes and Records, 1956, No. 43, p. 10, Msimjiri, Rondo Plateau, southeastern Tanganyika.
- 1959 Typhlops tettensis rondoensis Loveridge, Proc. Zool. Soc. London, vol. 133, p. 38, Mtene, Rondo Plateau, southeastern Tanganyika.
- 1959 Typhlops tettensis tettensis (non Peters): Loveridge (part), Proc. Zool. Soc. London, vol. 133, p. 37, Mihuru near Newala, southeastern Tanganyika.

Description. Brown above, with a yellow spot on each scale (generally on the anterior part of the scale, instead of the posterior part as in *tanganicanus*), below uniform yellowish. One specimen with spotted pattern. Scale rows: 24-22-20 to 26-24-22. Number of scales between the preocular and the tip of the tail: 314-353 (without sexual difference). Prefrontal broad, subtrapezoidal but rounded. Supraocular oblique, but with curved external border, its apex between the nasal and the preocular. Eye *in front* of the posterior border of the preocular. Nasal suture proceeding from the 1st labial. Preocular in straight contact with only the 2nd upper labial (however, it is wedged between the 2nd and 3rd labials in the Msinjiri specimen). Ocular wedged between the 2nd and 3rd labials, the lower part sometimes separated. Diameter of body 30 to 39 times, width of head 41 to 57 times, in the total length. Size small, up to 370 mm.

Distribution. Rondo Plateau and Newala region in southeastern Tanganyika.

Specimens examined. Tanganyika. Nchingidi, Rondo Plateau: MCZ 48066 (type), 48067-68 (paratypes). Msinjiri: MCZ 54510. Newala: MCZ 57184-86. Mtene: MCZ 57187-88.

Remarks. The Newala specimens previously referred to *tettensis* by Loveridge (1959) have really the *rondoensis* correlation of characters: white belly, same location of the eye, same connections of the preocular and ocular with the labials.

 $^{1\,{\}rm In}$ this specimen, the ocular is wedged between the 2nd and 3rd labials as in T. rondoensis.

TYPHLOPS OBTUSUS Peters

- 1865 Typhlops (Onychocephalus) obtusus Peters, Monatsb. Akad. Wiss. Berlin, p. 260, pl., fig. 2, Shire River, Nyasaland.
- 1893 Typhlops obtusus: Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 38, Shire valley and Nyasaland.
- 1953 Typhlops tettensis obtusus: Loveridge, Bull. Mus. Comp. Zool., vol. 110, p. 243, Cholo Mtn., Mlanje Mtn., Nyasaland.

Description. Dorsal scales brown or blackish, whitish at the base, darker on the sides; lower parts whitish. Scale rows: 24-22-20 to 28-25-22. Number of scales between the prefrontal and the tip of the tail: 417-484 (apparently without sexual difference). Prefrontal rather narrow, subhexagonal. Supraocular transverse, its lateral apex wedged between the preocular and the ocular. Eyes not distinguishable. Preocular wedged between the 2nd and 3rd labials. Nasal suture proceeding from the 1st labial. Diameter of body 48 to 76 times, width of head 70 to 86 times, in the total length. Size small, up to 350 mm (391 mm on freshly killed material, fide Loveridge).

Distribution. Nyasaland.

Specimens examined. Nyasaland. Mlanje Mtns.: MCZ 51027-29. Cholo Mtns.: MCZ 51025-26.

Remarks. T. decorosus Buchholz and Peters has been claimed (Loveridge, 1953) to be very nearly related to *obtusus*. I have compared the MCZ specimens of *obtusus* with three individuals of *T. decorosus:* two from Sakbayene, Cameroon (MCZ 14994, 22829) and one from Metet, Cameroon (MCZ 13227). Both species are very slender, but they differ widely in other characters; the preocular is in straight contact with the labials in *decorosus* and, what is far more important, the head scale pattern is entirely distinct from what we can see in all the species of the *punctatus* group. In *decorosus*, the supraocular is in very short contact with the ocular and with the nasal. Hence the following ratios are very characteristic of *decorosus*, when compared with all the species examined here:

a) The length of contact of the supraocular and the nasal in per cent of the length of the prefrontal: ± 20 per cent in *decorosus*, 50 to 160 per cent in the others.

b) The contact of the nasal with the prefrontal is more than $1\frac{1}{2}$ times as long (± 180%) as that with supraocular in *decorosus* while it is at most $1\frac{1}{2}$ times as long and often shorter in the other species.

c) The same contact is more than twice as long (230%) as the contact between the supraocular and the ocular in *decorosus*, while it is shorter in the other species.

It seems to me that T. decorosus is related to the colorless species group of which T. coecus is the oldest known representative.

Typhlops fornasinh Bianconi

- 1847 Typhlops fornasinii Bianconi, Spec. Zool. Mosamb., p. 13, pl. III, fig. 1, Mozambique.
- 1854 Onychocc phalus mossambicus Peters, Monatsb. Akad. Wiss. Berlin, p. 621, Insulae Mozambique and Anjoan.
- 1854 Onychocephalus trilobus Peters, Monatsb. Akad. Wiss. Berlin, p. 621, Inhambane, Mozambique.
- 1860 Onychocephalus tettensis Peters, Monatsb. Akad. Wiss. Berlin, p. 80, Tete, Mozambique.
- 1882 Typhlops tettensis: Peters, Reise nach Mossambique, vol. 3, p. 92, pl. XV, fig. 1.
- 1882 Typhlops mossambicus: Peters, Reise nach Mossambique, vol. 3, p. 93, pl. XV, fig. 2.
- 1882 Typhlops fornasinii: Peters. Reise nach Mossambique, vol. 3, p. 94, pl. XV, fig. 3.

Description. Dark brown, bluish or greyish, often with anal region and lower surface of head yellowish. Scale rows: 26-24-22. Number of scales between the prefrontal and the tip of the tail: 252-272. Prefrontal small, rounded. Supraocular transverse, its lateral apex between the preocular and the ocular. Eyes behind the posterior border of the preocular. Nasal suture proceeding from the 1st labial. Preocular wedged between the 1st and 2nd upper labials. Diameter of body 23 to 38 times, width of head 47.4 times (one cotype of mossambicus), in the total length. Size very small, up to 170 mm.

Distribution. Mozambique.

Specimens examined. Mozambique. MCZ 21007 (cotype of mossambicus Peters). Inhambane: MCZ 21006 (cotype of trilobus Peters). Lorenco-Marques: MCZ 41946-49.

Remarks. This species differs from all the forms involved in the T. *punctatus* complex, by its small size, its almost uniformly dark coloration, its small rounded prefrontal and its low number of scales between the prefrontal and the tip of the tail.

It is fortunate that Peters gave the latter figures, since we can now be sure that his *tettensis* has nothing to do with the form to which Loveridge (1942) erroneously gave this name. The alleged differences between *tettensis*, mossambicus and fornasinii are triffing in comparison with what they have in common, and they are here considered as individual variations.

TYPHLOPS STEINHAUSI Werner

- 1909 Typhlops steinhausi Werner, Mitt. naturh. Mus. Hamburg, vol. 26, p. 209, Kamerun.
- 1911 Typhlops batesi Boulenger, Ann. Mag. Nat. Hist., (8) vol. 8, p. 370, Bitye, Cameroon.

1923 Typhlops intermedius (non Jan): Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 47, Niangara, northeastern Congo.

Description. Gray above, with a yellowish spot, corresponding to each scale; venter uniform yellow. Scale rows: 24-25-23 to 26-26-24. Number of scales between the prefrontal and the tip of the tail: 402-425 (without difference between the sexes). Prefrontal small, subhexagonal. Supraocular transverse, its lateral apex between the preocular and the ocular. Eyes below the preocular or indistinct. Nasal suture proceeding from the 1st labial or from its suture with the rostral. Preocular in straight contact with three labials (1st, 2nd and 3rd). Diameter of the body 40 to 51 times, width of head 50 to 62 times, in the total length. Size rather small, up to 410 mm.

Distribution. Northern part of the rain forest from Cameroons to Ituri.

Specimens examined. Cameroon. Bitye: MCZ 11294, AMNH 7682-83. Kribi River: CNHM 4034. Lolodorf: MCZ 9242. Congo. Niangara, Ituri: AMNH 11630-31.

TYPHLOPS ANGOLENSIS Bocage

This species has been often mistaken for others: *punctatus* and *intermedius* (cf. Schmidt 1923) in the western and southern parts of its range and for *blanfordi* (which is indeed one of its geographical races) in the northeastern part of its range. Its geographical variation is considerable and has added to the past confusion of the group.

It can be easily distinguished from T. punctatus, T. boulengeri, T. schmidti, T. gierrai, and T. rondoensis by the shape and relations of the prefrontal and the supraocular; the same species (except rondoensis) are also different in the location of the eye, as is T. congestus which can further be distinguished from T. angolensis by its thickness. T. obtusus is, on the contrary, more slender than any population of angolensis, and T. fornasinii is very different in its size and its small longitudinal count of scales.¹ A spotted

¹ *T. steinhausi* is closely related to *T. angolensis* and must have been the northwestern subspecies of this Rassenkreis in the relatively recent past. The only character by which *T. steinhausi* can be distinguished from all races of *T. angolensis* is the fact that the preocular is in contact (straight) with three upper labials (1, 2, 3) instead of two.

pattern such as many species have with a varying frequency is never encountered.

Key to the subspecies of Typhlops angolensis

- Belly entirely or almost entirely light colored: color pattern similar in young and adults. Western populations.
 Belly brown colored (scales brown on the borders) except, in some forms, for a midventral light band. Young dark colored except for the buccal and anal regions and sometimes for the midventral zone. Oriental races.
- Preocular wedged between the 2nd and 3rd labials.
 Preocular in straight contact with the 2nd and 3rd labials; 30 to 36 midbody scale rows. Diameter of body 29 to 47 times, width of head 51 to 68 times, in the total length. Eastern slopes of Mount Kahusi, Bukavu region, Kivu, eastern Congo. Rugege Forest, Ruanda.
 T. angolensis irsaci Laurent

- Preocular generally wedged between the 2nd and 3rd labials. No midventral light zone. Midbody scale rows 26 to 32 (generally 30). Lowland in savanna regions from eastern Congo, southeastern Congo, Ruanda Urundi, Kenya and northern Angola.

T. angolensis adolfi Sternfeld Preocular always wedged between the 2nd and 3rd labials. Central part of the belly light colored. Midbody scale rows 28 to 32 (generally 30). Southern part of Itombwe Mtns., Kivu.

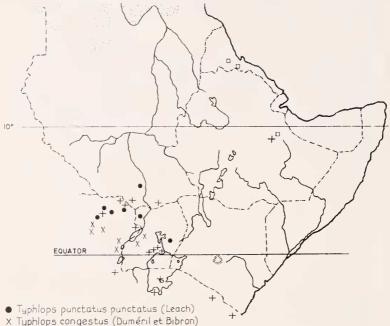
T. angolensis symoensi Laurent Preocular generally in straight contact with the 2nd and 3rd labials. No midventral light zone. Scales between the prefrontal and the end of the tail, 411 to 573. Mountain savannas of the eastern Congo, Uganda and Ruanda-Urundi; Rwindi and Ruzizi Valleys.

6.

T. angolensis dubius Chabanaud¹ Preocular in straight contact with 2nd and 3rd labials. Midventral light zone present or absent. Scales between the prefrontal and the end of the tail, 347 to 392. Eritrea and Ethiopia.

..... T. angolensis blanfordi Boulenger

1 Between dubius and adolf the cline in midbody scale rows is smooth enough to make the synonymy of dubius an arguable alternative to its recognition. In such a case, however, the striking altitudinal cline must be embodied in the diagnosis of adolf; symmensi could possibly be similarly treated. Likewise, polylepis and *irsaci* could be regarded as exemplifying similar orophilous trends and thus could be included with the typical form. However, evidence of a smooth cline is definitely lacking for *irsaci*.



+ Typhlops boulengeri boulengeri Bocage

Typhlops angolensis blanfordi Boulenger

Map 5. Distribution of species of the Typhlops punctatus group in northeast Africa.

SUMMARY SYNONYMY OF THE SUBSPECIES OF T. ANGOLENSIS

TYPHLOPS ANGOLENSIS ANGOLENSIS Bocage1

- 1866 Onychocephalus angolensis Bocage, Jorn. Sci. Lisboa, vol. 1, p. 46, p. 65, Duque de Bragança, Angola.
- 1887 Typhlops (Onychocephalus) congicus Boettger, Zool. Anz., vol. 10, p. 650, Povo Netonna, near Banana, Congo.
- 1923 Typhlops intermedius (non Jan): Schmidt (part), Bull. Amer. Mus. Nat. Hist., vol. 49, p. 47, west of Fort Beni, Akenge, Medje, Niapu, Stanleyville, Congo.
- 1923 Typhlops tornieri (non Sternfeld): Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 49, p. 50, Stanleyville, Congo.

¹ Additional specimens: Lukolela, western Congo (AMNII 45912); Omboue, Gaboon (USNM 62146); Canzele, Angola (CNHM 74243).

- 1940 Typhlops punctatus punctatus (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Lukolela, western Congo.
- 1956 Typhlops angolensis angolensis: Laurent, Ann. Mus. Congo. Zool., in octavo, vol. 48, p. 55, Kikungwa, Kamituga, Manguretshipa, Angumu, Kamande, eastern Congo (which see for a more complete synonymy).

TYPHLOPS ANGOLENSIS ADOLFI Sternfeld¹

- 1910 Typhlops adolfi Sternfeld, Mitt. Zool. Mus. Berlin, vol. 5, p. 70, Fort Beni, Kivu, eastern Congo.
- 1935 Typhlops kaimosae Loveridge, Bull. Mus. Comp. Zool., vol. 79, p. 5, Kaimosi, Kenya.
- 1940 Typhlops punctatus punctatus (non Leach): Bogert (part), Bull. Amer. Mus. Nat. Hist., vol. 77, p. 14, Chogoria, Kenya.
- 1956 Typhlops angolensis adolfi: Laurent, Ann. Mus. Congo, in octavo, vol. 48, pp. 63, 349, figs. 5-6, Beni, Uvira, Nyunzu, "Ituri", Djalasinda, Kilo, Nizi, Geti region, Tembwe, Mpala, Kabambare, Blukwa, eastern Congo; Nyakatare, Ngarama, Rwankuba, Nyarutunga, Lake Tshohoha, Kabuyenge swamps, Mugera Rusengo, Kiharo, Makamba, Gabiro, Chinzowe, Kakitumba, Ruanda-Urundi (which see for a more complete synonymy).
- 1960 Typhlops angolensis adolfi: Laurent, Ann. Mus. Congo, in octavo, vol. 84, p. 15, Kakitumba, Ruanda; Uvira, Lubondja, eastern Congo.
- TYPHLOPS ANGOLENSIS DUBIUS Chabanaud
- 1916 Typhlops dubius Chabanaud, Bull. Mus. Hist. Nat., vol. 22, p. 364, figs. 1–3, volcans du Kivori (for Kivu volcanoes).
- 1933 Typhlops lestradei Witte, Rev. Zool. Bot. Afr., vol. 23, p. 207, figs.
 1-3, Rubengera, Ruanda.
- 1935 Typhlops blanfordii (non Boulenger): Pitman, Uganda Journal, vol.
 3, p. 146, Mushongero, Lake Mulanda, Uganda.
- 1942 Typhlops blanfordii lestradei: Loveridge, Bull. Mus. Comp. Zool., vol. 91, p. 254, pl. 2, Mushongero, Nyakabande, Uganda; Kisenyi, Ruanda; Upper Mulenga, Idjwi Id.
- 1952 Typhlops ochraceus: Laurent, Rev. Zool. Bot. Afr., vol. 46, p. 269, Mulenge, Lulenga, eastern Congo.
- 1956 Typhlops angolensis dubius: Laurent, Ann. Mus. Congo Zool., in octavo, vol. 48, p. 60, Mabenga, Tshanzerwa, Rutshuru, Tshumba, Munagana, Lulenga, between Bobandana and Kisenyi, upper Mulinga, castern Kivu; Astrida, Ngozi, Murehe, Ruanda-Urundi; p. 349, Malambo, Bushovu, Idjwi Island, eastern Congo (which see for other quotations).
- 1960 Typhlops angolensis dubius: Laurent, Ann. Mus. Congo Zool., in octavo, vol. 84, p. 14, south Idjwi Island, Luvungi, Luberizi, Remera, Runingo, eastern Congo; Astrida, Bubanza, Ruanda-Urundi.

¹ Additional specimens seen: Mt. Kenya (AMNH 2279); Chigoria, Kenya (AMNH 51939).

TYPHLOPS ANGOLENSIS POLYLEPIS Laurent

- 1956 Typhlops angolensis polylepis Laurent, Ann. Mus. Congo Zool., in octavo, vol. 48, p. 56, fig. 6, pl. VII, fig. 3, Kiandjo, Tubutubu, Kalondo, eastern Congo.
- 1956 Typhlops congicus lestradei: Laurent (part, non Witte), Ann. Mus. Congo Zool., in octavo, vol. 48, p. 74, Burunga, eastern Congo.
- 1960 Typhlops angolensis angolensis: Laurent (non Bocage), Ann. Mus. Congo Zool., in octavo, vol. 84, p. 10, Tshabondo, eastern Congo.
- 1960 Typhlops angolensis polylepis: Laurent, Ann. Mus. Congo Zool., in octavo, vol. 84, p. 13, Luemba, eastern Congo.

TYPHLOPS ANGOLENSIS IRSACI Laurent

- 1956 Typhlops angolensis irsaci Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 57, p. 349, figs. 3–4, 6, pl. VII, fig. 4, Lwiro, Mt. Kahusi, Hongo, Bukavu, Katana, Ibanda, eastern Congo; Rwasenkoko, Ruanda.
- 1956 Typhlops congicus lestradei: Laurent (part, non Witte), Ann. Mus. Congo, Zool., in octavo, vol. 48, p. 74, Bukavu, p. 350, Lwiro, eastern Congo.
- 1960 Typhlops angolensis irsaci: Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 12, Hombo, Lwiro, eastern Congo.

TYPHLOPS ANGOLENSIS SYMOENSI Laurent

1960 Typhlops angolensis symoensi Laurent, Ann. Mus. Congo, Zool., in octavo, vol. 84, p. 10, Ngovi River, Makobola, Fizi, eastern Congo.

TYPHLOPS ANGOLENSIS BLANFORDI Boulenger

1893 Typhlops blanfordi Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 39, pl. II, fig. 5, Senafe, Abyssinia.

PHYLOGENETIC RELATIONSHIPS

The *Typhlops punctatus* group can be defined by the following characters: Scale rows: 22 to 36. Ratio length/diameter 17 to 62. Preocular generally in contact with labials (separated by a small scale in *gierrai*), almost always in contact with 2nd labials, generally with the 3rd also, sometimes even with the 1st. Ocular in contact with labials. No subocular. Snout rounded or with an obtuse angle. Nostrils inferior. Rostral broad (more than a third the width of the head). Nasal cleft proceeding from the first labial, sometimes from the rostral, not extending to the upper surface of the head (individual exceptions to this last character in *T. fornosinii*). Tail broader than long.

We cannot be sure that the group here studied is a truly homogeneous assemblage; some species not considered here, such as T. bibroni, may belong here. However, some assumptions can be

```
L = longitudinal count of scales { o o
S = rows of scales around midbody
Ss = small size
Ms = moderate size
Ls = lorge size
D = ratio length/diameter
T = ratia length/width of head
P = punctate colour pattern
M = marmarate colour pattern
Vor____ = shape of contact between labials (generally 2-3) and preocular
I-2-3 = straight contact between preocular and three labials
∀ = small scale between preocular and labials
X = eve indistinct
Nor X or X = location of eye (behind, belaw, or in front of the rear border of the preocular)
O = thinner or slender
O = thicker
= light belly
= dark belly
= belly light in middle
entry or shape of prefrontal and supraocular
```

Fig. 5. The symbols listed above apply to Figures 6-9. In addition, certain combinations of symbols are used. Thus MSs means moderate to small size, and M and P combined, one letter larger than the other, indicates that both punctate and marmorate color patterns may exist in the same species, that indicated by the smaller letter being the less frequent. Parentheses around any symbol implies that that condition is exceptional in that species or group.

made. For instance, T, fornasinii which is rather different from all other forms, and may even be extraneous to the group, seems to be closely related to T. boettgeri from Madagascar; the case is paralleled by other forms, like Chamaeleon fischeri and C. bifidus. T. fornasinii may represent the first dichotomy of the group or an old offshoot of T. angolensis. T. angolensis must represent a very old speciation also, perhaps having arisen from a first montane differentiation. It seems likely that T. obtusus has been a secondary branching from this angolensis complex in southeastern Africa, and T. steinhausi a more recent one in the northern part of the rain forest.

T. boulengeri appears to result from a more recent splitting (savanna versus forest, or southern savanna versus northern savanna) with two successive montane and local differentiations in the eastern Tanganyika mountains: T. gierrai, which has reached specific status, and later T. b. usambaricus. Another

secondary offshoot of T. boulengeri is obviously T. schmidti but it is difficult to tell under what conditions the primary geographic differentiation occurred: T. schmidti is more southerly in distribution and partly sympatric with T. boulengeri but we have no reason whatever for supposing a forest or a montane origin. Much



Fig. 6. Dendrogram of the main phylogenetic relationships in the Typhlops punctatus group (sensu lato).

more likely is an intrasavanna cline followed by a breakup resulting from the extinction of intermediate populations. The complex comprising T. punctatus and T. congestus has very likely been a single species with specific isolation between the more distant subspecies, i.e. between punctatus and congestus, between which liberiensis intervenes. Subspecific relationships appear almost certain between punctatus and liberiensis. Indeed they could exist

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

between *liberiensis* and *congestus* and in this case, *congestus* would have to be considered as a subspecies of T. *punctatus*. But the evidence for species level relationships between T. *congestus* and the

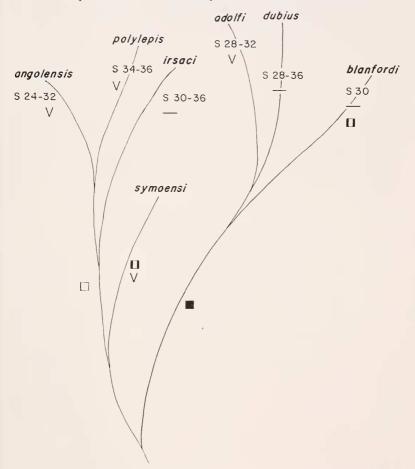


Fig. 7. Dendrogram of the phylogenetic relationships in Typhlops angolensis.

punctatus savanna populations and of a distributional gap between *congestus* and *liberiensis* suggests a complete specific separation.

However, it is impossible to tell whether the primary factor of speciation has been simple geographic isolation between the two

parts of the rain forest, i.e. between *liberiensis* and *congestus*, or geographic plus ecological isolation between savanna *punctatus* and forest *congestus*, or a distance effect between *punctatus* and *congestus* followed by a subsequent extension of range and thus a secondary meeting of these populations along the northern border of the eastern rain forest. Likewise, it is not clear whether this evolution started in a savanna environment (with *punctatus*) or in the forest (with *liberiensis* or *congestus*). Of course, the burrowing habits must have been often initiated as a protection against dryness, and accordingly such adaptations are more frequent in savannas. Hence, there is a slight presumption that *T. punctatus* is more primitive than the three other forms. However, the Typhlopidae, which are now cosmotropical and live in every environment, are so old a group that it is difficult to apply this principle safely to any particular phase of their history.

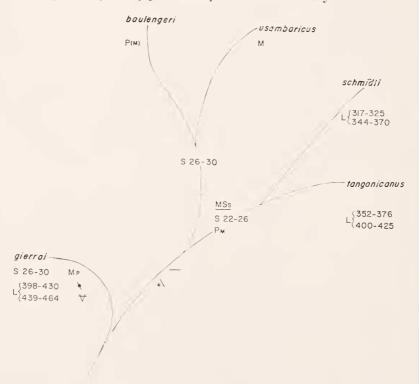


Fig. 8. Dendrogram of the phylogenetic relationships in the Typhlops boulengeri group.

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

The taxonomic characters are hardly useful in this connection because the primitive and secondary conditions cannot be easily distinguished. It may be assumed, however, that the number of scale rows is generally higher in primitive forms, while the longitudinal count is lower; and also that a lengthening of the body is secondary. However, some reversals of these trends are far from excluded, as is indeed obvious in the correlation of higher counts with altitude.

In the present case, eastern *congestus* is probably the most advanced type, since the unusual condition of the nasal suture is apparently secondary and it has only one color phase which, being less frequent than the uniform pattern in *Typhlops*, is probably secondary too. Which is the most primitive among the three forms is a mere guess; moreover it has little meaning, since each of these could have retained one primitive character.



Fig. 9. Dendrogram of the phylogenetic relationships in the Typhlops punctatus group (sensu stricto).

ARTIFICIAL KEY TO THE SPECIES OF THE TYPHLOPS PUNCTATUS GROUP

1.	Less than 280 scales between the prefrontal and tip of the tail. Mozambique. $T.$ fornasinii Bianconi More than 280 scales between the prefrontal and the tip of the tail.
2.	Less than 26 midbody scale rows. ¹
3.	Prefrontal subhexagonal; supraocular generally transverse, its lateral apex between preocular and ocular.
	Prefrontal subtrapezoidal; supraocular generally oblique, its lateral
4.	apex between nasal and ocular,
	Some eastern specimens of <i>T. congestus</i> Duméril & Bibron Prefrontal generally narrow. Eye under preocular, when visible. Di- ameter of body 26 to 76 times, breadth of head 37 to 86 times, in body length (see scatter diagrams). No spotted phase. Nasal suture proceeding from the 1st labial.
5.	 Eye visible (except in individuals before sloughing). Diameter of body 26 to 51 times, breadth of head 37 to 72 times, in body length. Between the prefrontal and the tip of the tail, 323 to 425 scales6 Eye always hidden. Diameter of body 48 to 76 times, breadth of head 70 to 86 times, in body length. Scales between the prefrontal and the tip of the tail, 417 to 484. Nyasaland and Mozambique
6.	Preocular in straight contact with 1st, 2nd and 3rd labials. Diameter of body 40 to 51 times in body length. More than 400 scales between prefrontal and the tip of the tail. Cameroon to northeastern Congo. T , steinhausi Werner
	Preocular wedged between the 2nd and 3rd labials. Diameter of body 26 to 40 times in body length. Less than 375 scales between the
	prefrontal and the tip of the tail. Forest in Congo and Angola.
7.	Eye below the ocular
	T. rondoensis Loveridge
8.	Ventral coloration lighter than dorsal coloration but not sharply de- limited. Preocular in contact with 2nd labial, or 2nd and 3rd labials,

¹ Specimens with 24 midbody scale rows are very rarely encountered in *boulengeri* and in eastern populations of *congestus;* they are infrequent in *T. angolensis angolensis;* in *steinhausi,* two specimens out of seven have 25 midbody scale rows. Generally, all these forms have at least 26 midbody scale rows. In *schmidti,* on the contrary, individuals with 26 midbody scale rows are rare; the normal figures are 22 or 24.

rarely with 3 labials. Scales between the prefrontal and the tip of the tail, 343 to 400 (343-393 & &) (384-400 9 9). Generally more than 26 scale rows at midbody. Circum-forest distribution. T. boulengeri boulengeri Bocage Ventral coloration lighter than dorsal coloration, but not sharply delimited. Preocular generally in contact with 2d and 3rd labials. Scales between the prefrontal and the tip of the tail, 351 to 376 ($\beta \beta$), 400 to 425 (QQ). Midbody scale rows 22-24. Southeastern Tanganyika (allopatric to boulengeri). T. schmidti tanganicanus Laurent Ventral coloration lighter than dorsal coloration and sharply delimited. Preocular generally in contact with 2nd and 3rd labials. Scales between the prefrontal and the tip of the tail: 317-325 (2 & &), 344-370 (2 Q Q). Midbody scale rows 22-24 (rarely 26). Southeastern Congo, northern Angola and northern Rhodesia.T. schmidti schmidti Laurent An intercalary scale between the preocular and the 2nd and 3rd labials. Eye below the superficial suture between preocular and ocular. Usambara and Uluguru Mountains.T. gierrai Mocquard No such scale between the preocular and the labials. Eye generally below the preocular or the ocular.10 Prefrontal subhexagonal; supraocular generally transverse, its apex be-Prefrontal subtrapezoidal; supraocular generally oblique, its apex between nasal and preocular (between preocular and ocular however Prefrontal generally broad. Eye under ocular rather than under preocular. Diameter of body 17 to 30, breadth of head 27 to 47, times in body length (see scatter diagrams). A spotted phase frequent, even exclusive in eastern populations. Rain forest in Cameroon-Prefrontal generally narrow. Eye under preocular when visible. Diameter of body 25 to 51 times, breadth of head 37 to 75 times, in Preocular in contact with 2 labials. Nasal in contact with 2nd labial. Angola to Eritrea through Congo and Kenya. Preocular in contact with 3 labials. Nasal not in contact with 2nd labial. Cameroon to northeastern Congo.T. steinhausi Werner Preocular wedged between the 2nd and 3rd labials. Spotted phase Preocular in straight contact with the labials. Spotted phase infre-Midbody scale rows 30-34. Belly hardly less dark than the back or spotted like the back. Savanna regions between the Sahara and the rain forest, from Senegal to Sudan. T. punctatus punctatus (Leach) Midbody scale rows 26-30. Belly light colored. Western rain forest

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10.

11.

12.

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14.

(Guinea to Ghana).T. punctatus liberiensis (Hallowell)

.....T. boulengeri usambaricus Laurent

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hunN	Taxon, and number of specimens	in parentheses	T.p.punctatus (15)	T.p. liberiensis (27)	T.congestus (55)	T.b.boulenaeri (90)	T.b.usambarieus (2)	T.gierrai (9)	T.s.tanganicanus (10)	T.s.schmidti (20)	T.rondoensis (10)	T. fornasinii (6)	T. obtasus (5)	T.steinhansi (7)	T.a.angolensis (32)	T.a.adolfi (43)	T.a.dubius (64)	T.a.symocnsi (8)	T.a. polylepis (5)	T.a.irsaci (44)	T.a.blanfordî (2)

TABLE 1

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

TABLE 2

Difference between the number of scale rows at midbody and behind the head in *Typhlops* of the *punctatus* group. (Modal condition in bold face)

]	Reduc	tion				Incre	ase	
	1	-3	-2	-1	0	+1	+2	+3	+4
T.p.punctatus (14)			27		27	13	33		
T.p.liberiensis (27)	3	-1	41	15	22	11	4		
T.congestus (55)	27	7	49	4	13				
T.b.boulengeri (66)	2	2	18	8	56	5	9		
T.b.usambaricus (2)			50	50					
T.gierrai (9)			22	11	45	22			
T.s.tanganicanus~(10)		10	50		40				
T.s.schmidti (10)	60		30		10				
T.rondoensis (10)			-40		60				
T.fornasinii (6)			17		50		33		
T.obtusus (5)	20	20	60						
T.steinhausi (7)				14		29	57		
T.a. angolensis (32)	3		23	6	49	8	11		
T.a.adolfi (40)			5		63	3	27		2
T.a.dubius (47)			4	2	45	4	34	2	9
T.a.symoensi (5)						20	80		
T.a. polylepis (4)					25	25	50		
T.a.irsaci (44)			-1	7	67	20	2		
T.a.blanfordi (2)					100				

T. boulengeri is well distinguished by this character from *punctatus*, *liberiensis* and *congestus*; the same is true for *schmidti* compared with *tanganicanus*.

TABLE 3

Difference in the number of scale rows between the preanal region and the midbody region in *Typhlops* of the *punctatus* group. (Modal condition in bold face)

	<mark>-9</mark>	-8	-7	-6	-5	-4	-3	-2	-1	0
T.p.punctatus (14)		7		64		29				
T.p.liberiensis (27)		-1	4	15	22	44	7	4		
T.congestus (55)	2	-1	7	<u>58</u>	9	18				
T.b.boulengeri (63)				16	8	49	3	22		2
T.b.usambaricus (2)				50		50				
T.gierrai (9)				11		11	22	45	11	
T.s.tanganicanus (10)						20	20	60 <mark>-</mark>		
T.s.schmidti (10)						40		60		
T.rondoensis (10)						30		60		10
T.fornasinii (6)						33		50		17
T.obtusus (5)							20	60		20
T.steinhausi (7)							14	57	29	
T.a.angolensis (32)				19	6	60	6	9		
T.a.adolfi (40)				17	3	60		20		
T.a.dubius (47)		2	2	15		62		19		
T.a.symoensi (5)				80		20				
T.a. polylepis (4)				25		50		25		
T.a.irsaci (44)		2		20	2	54	2	20		
T.a.blanfordi (2)				50		50				

	Sex Unknown	363 - 416(3)	331 - 381(7)	351 - 400(15)		421 - 435(2)			321 - 345(3)	$252-272(8)(\mathrm{m}=261.9)^2$	417 - 484(3)		347	$411-573(14)(m = 484.7)^3$			419	
Number of scales between the prefrontal and the end of the tail. ¹	Females	399-428(8)(m = 415) 371-435(14)(m = 392.1)	341 - 410(15)(m = 376.1)	384-401(11)(m = 391.8)		439 - 464(2)(m = 451.5)	400 - 425(6) (m = 411.5)	344-370(2)(m = 357)	314-350(3)(m = 335.7)	255(1)	465(1)	405 - 419(4)(m = 412.3)	287 - 364(8)(m = 328.4)		520(1)			
Number of scales between the p	Males	376-403(3)(m = 392.3) 339-385(11)(m = 362.3)	322-378(18)(m = 350.3)	3.43-393(11)(m = 368.5)	344-390(2)(m=367)	398-430(5)(m = 411.4)	352-376(4)(m = 369.3)	317 - 325(2)(m = 321)	319-353(4)(m = 337.5)		467(1)	402 - 425(3)(m) = 415.7)	281 - 371(12)(m = 342.1)	425(1)	425 - 485(2)(m = 455)	347-392(2)(m = 369.5)	381-391(2)(m = 386)	
		T.p.punetatus T.p.liberiensis	T.congestus	T.b.boulengeri	T.b.usambaricus	T.gierrai	T.s.tanganicanus	T.s.schmidti	T. rondocnsis	T. for nasini i	T.obtusus	T.steinhausi	T.a. angolensis	T.a.dubius	T.a.irsaci	T.a.blanfordi	T.a.adolfi	

TABLE 4

isi 1 This character has generally been omitted from descriptions and other reports on Typhlops because the count is very laborious. However, it undoubtedly taxonomically useful and even seems to be the only character correlated with sex in most forms. Unfortunately, I can rely here only (the data of material in nuscemns in the United States, but the results are convincing enough. It is a first of a cost of material in success in the United States, but the results are convincing enough. The variation of dubius is particularly striking and suggests an altitudinal **d**ine, as for the number of scale rows.

TABLE 5

Labials touching the preocular in Typhlops of the *punctatus* group, frequency in per cent

	0	1 - 2	1 - 2 - 3	2	2 - 3	
T.p.punctatus (14)				-1	96	
T.p.liberiensis (27)		2		2	96	
T.congestus (12)					97	
T.b.boulengeri (57)		29	2	37	32	
T.b.usambaricus (2)					100	
T.gierrai (9)	100					
T.s.schmidti (10)				10	90	
T.s.tanganicanus (10)				10	90	
T.rondoensis (10)				90	10	
T.fornasinii (6)				100		
T.obtusus (5)					100	
T.steinhausi (2)			100			
T.a.angolensis (28)					100	
T.a.adolfi (41)	2				98	
T.a.dubius (47)					100	
T.a.symoensi (5)					100	
T.a. polylepis (4)					100	
T.a.irsaci (46)					100	
T.a.blanfordi (2)	25			25	50	

442

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TABLE 6

Ratio between length of body and its diameter in *Typhlops* of the *punctatus* group.

$ \begin{array}{llllllllllllllllllllllllllllllllllll$			W)	(Modal condition in bold face)	ndition 1	plod f	ace)						
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		16	20	24	28	32	36	40	11	48	52	56	60
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$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		20	24	28	32	36	40	tt	48	52	56	00	64
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.p.punctatus (14)			40	40	13		2					
	T.p.liberiensis (27)		က	45	34	11	2						
	T.congestus (54)	15	41	37	2								
	T.b.boulengeri (76)			31	36	24	x	1					
	T.b.usambaricus (2)			50	50								
	T.gierrai (9)				11	34	22	33					
	T.s.schmidti (9)		11	12	22	22	22	11					
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.s.tanganicanus (10)				10	40	20	20	10				
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.rondoensis (9)				22	23	55						
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.fornasinii (6)			33	17	33	17						
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.obtusus (5)									40	40		20
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	T.steinhausi (7)						43	29	14	14			
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	T.a.angolensis (32)			16	47	28	9	ಣ					
16 23 36 20 5 12 38 25 25 20 20 40 20 14 23 38 16 5 100	T.a.adolfi (47)			2	+	28	24	26	12	÷			
12 38 25 25 20 20 40 20 14 23 38 16 5 100	T.a.dubius (44)				16	23	36	20	ũ				
20 20 40 20 2 14 23 38 16 5 100	T.a.symoensi (8)					12	38	25	25				
2 14 23 38 16 5 100	T.a. polylepis (5)				20	20	40	20					
2)	T.a.irsaci (44)			5	14	23	38	16	ũ	¢1			
	T.a.blanfordi (2)				100								

LAURENT: REVISION OF TYPHLOPS PUNCTATUS GROUP

TABLE 7

Ratio between the length of body and the breadth of the head in *Typhlops* of the *punctatus* group. This character is more reliable than the preceding, since the breadth of the head is not influenced by the physiological condition of the individual. On the other hand, some species have larger heads than others. (Modal condition in bold face)

	$\frac{20}{28}$	28– 36	36– 44	44– 52	52 - 60	60– 68	68– 76	76– 84	$\frac{84-}{92}$
T.p.punctatus (12)		8	9	50	33				
T.p.liberiensis (27)		3	50	27	20				
T.congestus (50)	.1	38	48	10					
T.boulengeri (63)		9	33	45	13				
T.b.usambaricus (2)			100						
T.gierrai (9)			22	34	44				
T.s.schmidti (9)			23	44	33				
T.s.tanganicanus (9)				20	70	10			
T.rondoensis (10)		10	20	30	40				
T.fornasinii (6)		33	34	33					
T.obtusus (5)							40	40	20
T.steinhausi (7)				14	72	14			
T.a. angolensis (28)			22	48	26	4			
T.a.adolfi (38)			7	27	37	24	5		
T.a.dubius (44)			7	24	41	26	2		
T.a.symoensi (8)			13	50	37				
T.a. polylepis (4)			25	25	25	25			
T.a.irsaci (44)			7	43	27	23			
T.a.blanfordi (2)				100					

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